

On the Genital System of *Lyctus brunneus* Steph., with a Note on *Lyctus linearis* Goeze (Coleoptera). By A. M. ALTSON, F.E.S. (Communicated by Dr. A. D. IMMS, F.L.S.)

(PLATES 31-34, and Text-figs. 1-4.)

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INTRODUCTION.

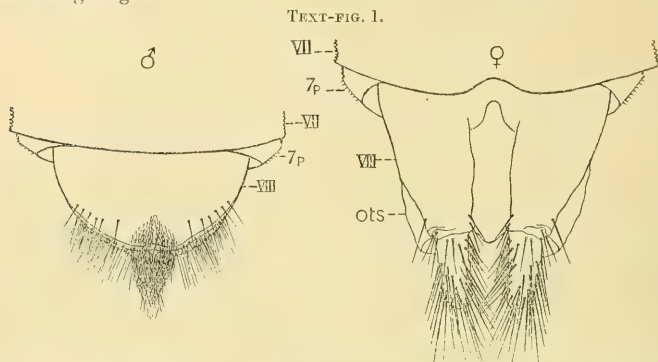
IN the following description of the genital system of *Lyctus brunneus* Steph., it has been found necessary to add a comparative description of part of the alimentary tract of both sexes; that of the male discloses nothing remarkable in the position of these parts, whereas that of the female is curiously situated, and appears to be only partially adapted to meet its particular method of oviposition.

Sharp and Muir (10) figure and describe the male genital tube of *L. linearis* Goeze (*canaliculatus* Fab.). Other than this, no reference to the genital system of either sex of any species of *Lyctus* has been found.

To complete the examination of the organs of the female *L. brunneus*, it was necessary to cut series of sections. Longitudinal and transverse sections were made of pupæ, immature and mature adults. "Immature adults" refers to beetles removed from their pupal chambers before either their integument had hardened or they had eaten any wood, *i. e.* between four and five days after shedding the pupal exuviae.

The beetles are not sexually mature until they are ready to emerge; mating invariably takes place at the earliest possible opportunity after that event.

The only secondary sexual characters observed were a difference between the ventral pygidial plates (VIII sternite) and between the apical margins of sternites VII (the 5th visible sternite of systematists) (text-fig. 1). Beyond these characters, unless the "ovipositor" or the œdeagus is extruded, or a pair are found in coition, it is impossible to distinguish the sexes externally, size being no guide.



Secondary sexual characters of *L. brunneus*. Male and female ventral pygidial plates. *ots*, base of outer sheath of ovipositor; VII, 7th sternite; *7p*, 7th pleurite; VIII, 8th sternite. *Camera lucida*, $\times 256$.

In the description of the male genital tube the nomenclature of Sharp and Muir (10) is followed, but in the case of the female reference was made to Packard (8), Berlese (2), Henneguy (3), and Stein (11) for terms applied to parts homologous to those found in *L. brunneus*.

TECHNIQUE AND METHODS.

The technique adopted to prepare the specimens for sectioning was similar to that employed by Awati (1). This method gave excellent results.

Fixation in Carnoy II for 24 hours; three to four hours after immersion in the fixative the head and most of the legs and the elytra and wings were cut off.

Dehydration in two washings of 90 per cent. alcohol, three hours; two washings in absolute alcohol, three hours; and one hour in a mixture of chloroform and absolute alcohol.

The object was next transferred to chloroform, in which it remained for two days; then into a cold saturated solution of paraffin-wax (58° C.) in chloroform, where it remained for two to three days. After this period the solution was warmed by standing it on top of the oven for 10 minutes, and the object was then transferred into pure molten wax (58° C.) for five to six hours.

A block was prepared in the usual way. The sections were stained in Ehrlich's Hæmatoxylin ($\frac{3}{4}$ hr.) and counter-stained in Picro-nigrosin (30 secs.).

MALE GENITAL SYSTEM.

The reproductive organs are shown in Pl. 31. fig. 1, and consist of the usual parts: testes (*ts*), vasa deferentia (*vd*), seminal vesicles (*sv*), accessory glands (*ag*), ejaculatory duct (*ej*), internal sac, median lobe (*ml*), and tegmen, comprising the lateral lobes (*ll*) and basal piece (*bp*).

There are six testicular follicles of unequal size attached to each vas deferens. They occupy a large area in the abdomen from the dorsal to the ventral surface, and extend from beyond the basal margin of the abdomen to the third sternite (Pl. 31. fig. 5). The testicular follicles are white, rounded and tapering towards their apex. There is a slight cavity in the centre of the base of each, whence a tube arises which joins the vas deferens, which is of variable thickness throughout its length. In repose the vasa deferentia are convoluted, in parts superimposed, and lie on the ventral surface. The vasa deferentia enter the seminal vesicles on their outer ventro-lateral margin (Pl. 31. fig. 4). The seminal vesicles are joined on their inner lateral surface for the greater part of their length; they are subcylindrical and rounded at their apices.

Arising from each seminal vesicle on its inner dorsal margin is a short tube; these tubes meet and form the ejaculatory duct. Superimposed and attached to the dorsal surface of each of the two short tubes is an accessory gland. The accessory glands are subcylindrical and curved, broadest towards their base and rounded at their apices.

The ejaculatory duct gradually tapers from its base until it enters the median lobe through the median foramen (*mf*), where it becomes hidden from view, emptying into the internal sac (*is*, Pl. 31. fig. 3). (It was not found possible to evaginate the internal sac, nor to kill a pair of beetles in coition with the organs *in situ*; but the internal sac was traced in sections of an immature male.)

The chitinized median lobe, viewed in section, is circular at its base and shortly becomes elliptical; towards its apex there arise on the upper dorsal and upper ventral surfaces a carina situated along the centre, with the internal sac lying over and on either side of the carina formed on the upper ventral surface (Pl. 31. fig. 2); the lower or outer ventral surface is convex at this point. The median orifice (*mo*, Pl. 31. fig. 3) is situated a little below the upturned point of the median lobe. Inside the median lobe are series of muscles and nerve-fibres (Pl. 31. fig. 2); one series of muscles is situated around the internal sac, others are attached to the walls of the lobe.

Encasing the median lobe on either side are the lateral lobes, which are roughly semicircular in section for the greater part of their length; they are

of a uniform thickness of chitin except towards their base, where the inner face becomes thin and flexible. Each lateral lobe contains a group of muscles and nerve-fibres extending to their apices (Pl. 31. fig. 2). At their base the lateral lobes become joined together ventrally and dorsally; at the latter point they join around the point of articulation (*pa*). Externally the median lobe and the lateral lobes bear sensory pits at their apices.

Enclosing the base of the lateral lobes is a thin piece of chitin, the basal piece (*bp*), which appears to clip the dorsal edges of the lateral lobes below the point of articulation. Arising from the surface of the basal piece towards its posterior margin is the flexible enveloping integument of the abdomen.

In sections of a male the spermatozoa were found in bundles, held together at their heads. In balsam mounts of the dissected genitalia these bundles could also be seen within the testicular follicles when the organs had been stained in hæmalum and indigo-carminé.

Between the dorsal pygidial plate (*dp*) and the œdeagus is a chitinous tube (*ev*) which completely envelops the anus (*an*) and anterior portion of the rectum (*r*) (Pl. 31. figs. 2 & 3). Each side of the chitinous tube (*ev*) invaginates to form a pair of stout rods (*vr*, fig. 3). These rods surround the œdeagus and abut at their base, which is towards the ventral surface of the abdomen. From the base of the rods there are three primary sets of muscles (*m*). Two of these sets follow the course of the rods and terminate around the chitinous tube; the third set runs between the rods and is attached to the enveloping integument below the base of the œdeagus; some of these muscles appear to be attached to the œdeagus ventrally.

From this it would appear that the latter muscles are primarily responsible for giving the œdeagus its necessary downward tilt preparatory to coition.

Following the alimentary tract back from the anus (*an*, Pl. 31. fig. 5) is the rectum (*r*), which is quite short and lies dorsal to the œdeagus and ejaculatory duct. Beyond the rectum is the colon (*cl*) lying dorsal to the accessory glands, part of the ejaculatory duct, and the seminal vesicles. Beyond the colon is the ileum, which disappears below the testicular follicles and lies towards the ventral surface of the abdomen. There are six malpighian tubes (*mp*) arising from the ileum, which at this point is lined with chitinized setæ. Beyond the ileum is the mesenteron (*ms*), which lies in the meta- and mesosternum, where it inclines towards the dorsal surface.

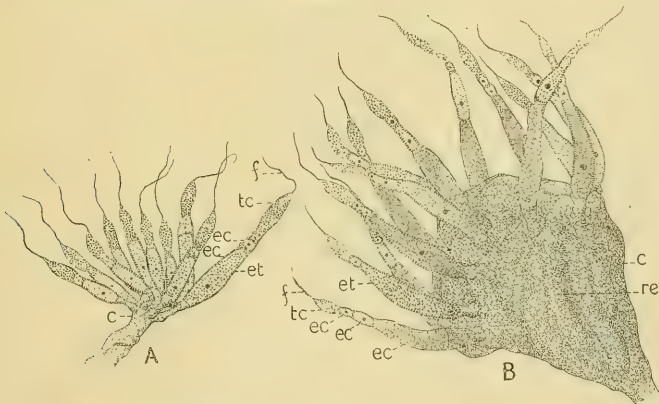
Arising from between the metathoracic acetabula (*mta*) is a "U"-shaped, strongly chitinized apodeme (*ap*); the base of the "U" arises from the metasternum (*q*), whilst the apices of the arms are held in position by muscles attached to the metanotum. From inside the "U"-piece and from its base arise two thin chitinous rods (*apr*). These rods traverse the floor of the metasternum and terminate above the metathoracic coxæ (*mc*), to which they are attached by radiating muscle-fibres.

A pair of glands or sacs (*sg*) disappearing beneath the œdeagus (*oe*) are shown (Pl. 31. figs. 1, 3, & 5). These glands unite and form a short narrow duct. When dissected out of a mature beetle the glands and duct are always found distended. The duct terminates abruptly between the 7th and 8th sternites. In section these glands are seen to be composed of cells containing very large nuclei. The function of the glands is not known; no odour other than that of the wood from which the beetles emerged was ever perceived. The glands are apparently pygidial glands (Berlese 2).

FEMALE GENITAL SYSTEM.

The reproductive organs of the female (Pl. 32. fig. 1) consist of two ovaries (*lo*, *ro*), two oviducts (*od*), a paired valve (*vl*), a spermatheca (*sp*) and spermathecal gland (*spg*), and a common oviduct (*co*) running into the sheaths of the "ovipositor," which terminates in the bursa copulatrix. In addition there is a long flexible cloacal stalk (*lr*) ("Kloakstiel," Stein 11) and two short rods (*sr*).

TEXT-FIG. 2.



A, the ovary of an immature female. B, the ovary of a mature unfertilized female, semi-diagrammatic. *c*, calyx; *ec*, egg-chamber; *et*, ovarian tube; *f*, filament; *tc*, terminal chamber; *re*, ripe eggs. *Camera lucida*, $\times 54$.

The ovaries (*lo*, *ro*) of a mature beetle each consist of fourteen ovarian tubes (*et*). Each tube consists of from four to five egg-chambers (*ec*), and a terminal chamber (*tc*) terminating in a filament (*f*). The ovarian tubes arise from an enlargement of the oviducts—the calyx (*c*). The calices act as receptacles for the ripe eggs, which pass into them from the basal egg-chambers. In fig. 1 (Pl. 32) there are three ripe eggs in the left calyx and two in the right.

It was found that the left ovary was always developed earlier than the right.

The ovary of an immature female examined consisted of only ten ovarian tubes (text-fig. 2, A), the other four eventually arising from the apex of the calyx and between the existing tubes. The ovary of a mature unfertilized female (text-fig. 2, B) shows a considerable enlargement of the calyx, which is tightly packed with ripe eggs.

From the calices the eggs pass along short oviducts into a double-chambered valve (*vl*). Each chamber of the valve is lined with brown chitinized setæ* with their free ends lying in the same direction as that in which the eggs pass (*vl*, Pl. 32. fig. 4). The chambers of the valve meet to form the commencement of the common oviduct, and the setæ terminate some distance before a valvular duct (*vt*) leading into the spermatheca enters the common oviduct.

The spermatheca is very large and terminates in a single tube—the spermathecal or accessory gland. In fertilized females the size of the spermatheca is perceptibly increased. Inside the spermatheca, arising from the ventro-lateral surface at the point (*psp*) where it narrows, are found a series of 27 chitinized setæ (*s*, Pl. 32. fig. 3); their function is obscure. The spermatozoa are mostly in packets—spermatophores (*spp*, Pl. 32. fig. 4),—but a considerable number are found loose in the fluid contents of the spermatheca.

The common oviduct, into which the eggs pass from the valves, is of muscular structure, and finally disappears into the “ovipositor.”

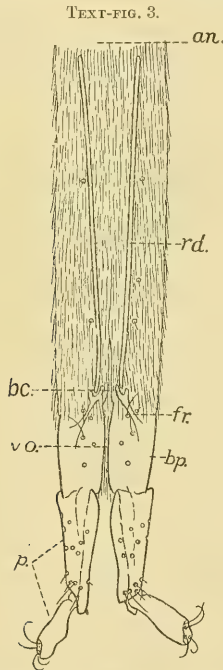
The long flexible cloacal stalk (*lr*, Pl. 32. fig. 2) arises from a point in the centre and near the base of the ventral pygidial plate (*vp*). The stalk extends through the middle of the abdomen into the meta-thorax to a point beyond the beginning of the “ovipositor,” where its apex enlarges into a knob from which two sets of muscle-fibres (m^1 , m^2) arise. The m^1 set of muscles consists of series of bundles of long fibres grouped around the “ovipositor,” and extending from the apex of the cloacal stalk to a point between the short rods (*sr*), where they are attached to the outer sheath (*ots*). The m^2 muscles surround the cloacal stalk to its base, where it is embedded in a mass of muscles. In addition to the muscles (m^1 , m^2), there is another series (m^3), which arise around the beginning of the “ovipositor” and completely surround the outer sheath, extending for about half its length, at which point they are attached to it. Further, there are numerous muscle-fibres arising from the same point as the (m^3) muscles; these are found longitudinally traversing the inside of the inner sheath (*ins*) of the “ovipositor” (Pl. 34. figs. 4-7). And, in addition, there is a series of cancellate muscles lining the walls of the distal portion of the “ovipositor,” apparently

* In a previous paper, “On the Method of Oviposition and the Egg of *Lyctus brunneus* Steph.” (Journ. Linn. Soc., Zool. xxxv. 1923, p. 217), the writer has stated that it is these setæ-lined valves which impart the striations and process to the deposited eggs.

to allow for its expansion during the passage of an egg. Another series of muscles (m^4) are found, arising from the lateral walls of the spermatheca and terminating around the common oviduct at a short distance from its base.

The common oviduct enters the "ovipositor" between the m^1 muscles.

When the ovipositor is in repose—as depicted in Pl. 32,—it consists of two sheaths, the outer or basal portion (*ots*), which is a transparent tube lightly chitinized, and the inner sheath or distal portion (*ins*), which is a continuation of the outer sheath. The two portions join at the point where the common oviduct enters. The surface of the distal portion of the "ovipositor"



Apex of the ovipositor, ventral. *an*, anus; *bc*, bursa copulatrix; *bp*, basal piece; *fr*, forked rod; *p*, vaginal palp; *rd*, chitinized rod; *vo*, vaginal orifice. *Camera lucida*, $\times 128$.

is covered with recumbent brown chitinized setæ, which extend as far as the bursa copulatrix (*bc*, text-fig. 3). The apex of the "ovipositor" (text-fig. 3) is stoutly chitinized, and consists of paired rounded basal pieces (*bp*), between which is the vaginal orifice (*vo*). Arising from each of the basal pieces is a

double-jointed vaginal palp (*p*), which bears a number of sensory pits. The inner lateral faces of the palps are concave. Within each basal piece is a short forked rod (*fr*), and articulating between the prongs of the fork and running back some distance is a chitinized rod (*rd*) ("Seitenstück," Stein 11).

The abdominal nerve-ganglion and commensures are not depicted; the latter were only traced to the venter of the spermatheca and to the valve.

The left top corner of Pl. 32, fig. 1 depicts a portion of the mesenteron (*ms*) terminating in the ileum (*lm*), from which arise six malpighian tubes (*mp*). The ileum, which is lined with chitinized setæ at its junction with the mesenteron, is followed by the colon (*cl*), which leads into the rectum (*r*). The rectum, which is of muscular structure, is visible for a considerable length before it—like the common oviduct—disappears into the "ovipositor." (In this figure the rectum has been pulled across to the left; it should lie looped over the "ovipositor" and enter from the right as in Pl. 33, fig. 2.)

Pl. 34 depicts the "ovipositor" in section. Figs. 4, 5, 6, and 7 are *camera lucida* drawings of transverse sections from an "immature" female. Fig. 4 shows the rectum (*r*) entering the inner sheath (*ins*) of the ovipositor from the right and assuming a position dorsal to the common oviduct (*co*), which enters from under the left. In fig. 5 the rectum (*r*) is now dorsal to the common oviduct (*co*), and both are completely enclosed by the inner sheath or distal portion (*ins*) of the "ovipositor," which in turn is enclosed within the outer sheath (*ots*). In fig. 6 the rectum (*r*) is seen emerging through the dorsal wall of the distal portion of the "ovipositor"; whilst in fig. 7 the rectum and anus (*an*) are now free of the inner sheath, which, at this point, becomes the integumental covering of the apex of the common oviduct (*co*) or bursa copulatrix.

Fig. 8 is a transverse section through the apex of the "ovipositor" of a fertilized female which had begun egg-laying. The section is about the beginning of the vaginal orifice (*vo*); it shows the stout outer lateral wall of the basal pieces (*bp*) and transverse muscles to allow of expansion.

Figs. 1, 2, and 3 are partially reconstructed *camera lucida* drawings of longitudinal sections of the "ovipositor" of a fertilized female that had been ovipositing. Fig. 1 shows the junction (*jo*) of the inner and outer sheaths, and the entry of the common oviduct from underneath to the ventral surface of the inner sheath and the position of the rectum. Fig. 2 is of a median section of the "ovipositor" showing the rectum convoluted (*rc*). Fig. 3 is a section through that part of the "ovipositor" where the rectum (*r*) emerges through the inner sheath.

The relative positions occupied by the genitalia and alimentary tract within the abdomen, meta- and mesothorax are depicted in Pl. 33, figs. 1, 2, and 3. No muscles are shown, as their inclusion would obliterate a large part of these organs. It will be seen that the female possesses an apodeme (*ap*) of a similar structure to that described in the male. The figs. 1 and 3 are based

on reconstructions made from a series of longitudinal sections of a fertilized female, and depict a left and right lateral view respectively, with the uppermost ovary and oviduct removed in each case. Fig. 2 is based on reconstructions made from balsam mounts of cleared specimens and from dissections, and depicts a dorsal view in which the relatively greater length of the rectum (r) of the female in comparison with that of the male (Pl. 31. fig. 4, r) is made apparent. The ratio is approximately 30 : 1.

Pl. 32. fig. 2 shows in longitudinal section the dorsal (dp) and ventral (vp) pygidial plates with the apex of the "ovipositor" between, and also part of the 7th sternite (VII), *i. e.* the 5th sternite of systematists.

The functioning of the parts of the ovipositor appear to be as follows:—

In repose (Pl. 32. fig. 1) m^1 , m^2 , and m^4 muscles are in a state of contraction, whilst m^3 and the longitudinal series within the inner sheath are in a state of expansion. By the contraction of m^3 , the outer sheath commences to collapse, the distal portion to issue from between the pygidial plates and drawing with it the muscular rectum and the common oviduct. By the simultaneous contraction of the muscles within the inner sheath, the outer sheath is caused to evaginate and issue from between the pygidial plates. The outer sheath continues to evaginate and issue until brought in check by m^1 muscles. When fully extruded the "ovipositor" is approximately the length of the female.

The withdrawal of the ovipositor is apparently achieved by the contraction of the expanded m^4 muscles, aided by the muscular common oviduct, which would pull back into its position of repose, bringing the distal portion of the "ovipositor" with it. Simultaneously, the contraction of m^1 muscles would pull back the basal part of the outer sheath, whilst m^3 muscles would draw into position the apical portion of the sheath.

As there are no muscles attached to the ileum, the colon, or the rectum, the resumption of the position of repose for this portion of the alimentary tract must be solely dependent upon the slight contraction of which the muscular rectum is capable—aided by the fixed mesenteron—and any tension that might be exerted by the ramifications of the trachea. That such is apparently the case is shown in Pl. 34. fig. 2. Here the rectum is seen convoluted—a condition that can only be attributed to an imperfect musculature.

Other sections of the same beetle disclosed two other points within the "ovipositor" where the rectum was similarly convoluted. In this condition no beetle could defæcate unless it extended its "ovipositor," and thus straightened the rectum. Whether this is ever done is not known. But as the food of these beetles consists of particles of wood, most of which appears in the frass never to be broken down, it is possible that penetration of the walls of the rectum and of those of the common oviduct may take place. And it seems probable that this defectiveness may be the cause of the death of quite a

number of beetles whose ovaries are found to contain a considerable portion of their complement of eggs. It has been observed that many beetles do expire with the "ovipositor" extruded—partially in the majority of cases.

When the distal portion of the ovipositor is gently pulled out by means of a fine pair of forceps from a freshly chloroformed beetle, the basal portion is seen to extend after the manner of a telescope.

Females have a gland on each side of the seventh abdominal segment correlated to the glands or sacs described in the male; and they are of similar structure. But in the females they do not meet, and from sections they appear to surround the tracheal trunks leading to the seventh abdominal spiracles.

COITION.

It has been mentioned that efforts to kill pairs in coition with the organs *in situ* failed to disclose more of the internal sac of the male than is shown in Pl. 31. fig. 2. And from the examination of the œdeagus the internal sac does not appear to be capable of evaginating more than half the length of the median lobe (Sharp & Muir 10).

In coition the beetles are superimposed, and the lateral lobes of the male assume an almost perpendicular position to the surface of the wood. As the beetles are very flat, the apices of the lateral lobes come in contact with the surface of the wood, and, if the female moves, as is frequently the case, the apices of the lateral lobes become bent and covered with particles of dirt and dust*.

NOTES ON THE GENITAL SYSTEM OF *LYCTUS LINEARIS* GOEZE.

An attempt has been made to carry out a comparative examination of the genital system of *L. linearis*. But no living specimens could be procured, and the following remarks are based upon the study of preparations made from the remains of the organs of dead beetles.

Two beetles—both males—were kindly sent by Dr. Hugh Scott, and three other specimens—one female and two males—were found in the pupal chambers in oak sent from Paris by M. P. Lesne. The oak was sent under the impression that it was infested by the larvæ of this species; however, as no beetles emerged within the normal period, it was broken up and no larvæ or pupæ were found.

The dead beetles obtained were first soaked for five days in water to which a few drops of formaldehyde were added. The specimens were then washed in water and dissected. The dissections were treated in the usual manner and mounted in balsam. The resulting preparations were moderately successful.

* From a control point of view, this is of considerable importance, for the treatment of the surface of the wood with an oleaginous or viscous substance causes the dirt and dust to adhere to such an extent as to jam the cedeagus—the lateral lobes become stuck to the median lobe, the median orifice becomes blocked, and the beetle is, as a result, killed.

One point observed was that the tergites of *linearis* were much more strongly chitinized than in *brunneus*, in which they are very flexible and only faintly discernible.

The male.—The œdeagus was found to agree with the description and figures of Sharp and Muir (10), except that the basal margin of the basal piece was found to terminate in front of the point of articulation, but not so far forward as in *brunneus*. Whether the anterior margin of the basal piece clipped around the lateral lobes was not observed, as no sections were made. In other respects it was similar, and gave the impression of being a more robust structure.

Nothing was found of the testes, but the position and appearance of the remains of the vasa deferentia, seminal vesicles, accessory glands, and ejaculatory duct were similar to those of *brunneus*.

The two rods arising from under the ejaculatory duct as in *brunneus*, and the "U"-shaped apodeme and apodemal rods were present.

The female.—The similarity of the extruded "ovipositor" as seen in dead females to that of *brunneus* has been referred to by others. From the preparation made, there were observed the setæ-lined valve and what would be the spermatheca and common oviduct. Remains of the ovaries were present, but the number of ovarian tubes could not be distinguished. The ovipositor, in repose, and the apex of the distal portion bore a marked similarity to those of *brunneus*. Further, the cloacal stalk and short rods, and the apodeme and apodemal rods were present.

From the appearance of the "ovipositor" in repose, it seems that the alimentary tract must follow a similar course to that of *brunneus*.

OBSERVATIONS ON STEIN'S 'FEMALE REPRODUCTIVE ORGANS IN COLEOPTERA.'

Stein (11), in his work on the genital system of Coleopterous females, describes and illustrates the organs of several species which in some particulars resemble the organs of *brunneus*. But this resemblance is so slight in most that no comparative deductions can be drawn. There are, however, a few points that call for comment.

The "ovipositor" in each of these cases consists of a tube ("Kloakrohr") which in repose telescopes approximately one-half within the other, but each varies in the appearance of the distal portion. In all cases the "ovipositor" is apparently shorter, in comparison to the length of the insect, than that of *brunneus* and *linearis*. The rectum, in each of the species referred to, enters the inner sheath of the "ovipositor" as in *brunneus*. The cloacal stalk is found, but it is not clear what distance within the abdomen it traverses, and in no case is there any indication of the short rods.

In the case of those females that are closely related systematically to the Lyctids, i. e. *Anobium punctatum* De Geer (*pertinax* F., *domesticum* Fourc.,

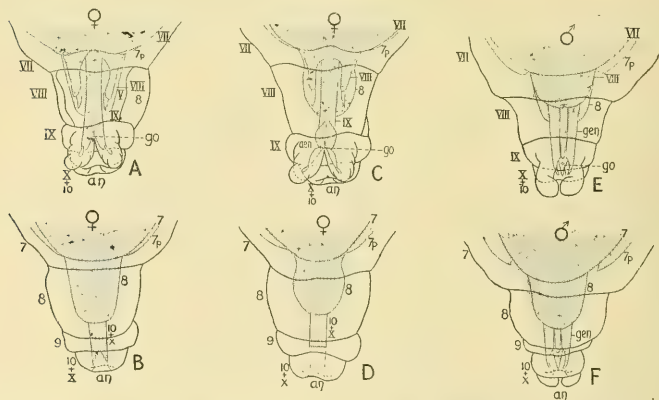
striatum Ol.), and *Cis boleti* Scop.*, the cloacal stalk, according to Stein, is dorsal to the "ovipositor," and it is therefore in a reversed position in *brunneus* and *linearis*. But in the case of other females somewhat distantly related systematically, such as *Helops (caraboides) Panz.) striatus* Fourc., *Edemera (virescens) lurida* Marsh, and *Cistela fusca*, the cloacal stalk, according to the same authority, lies below the "ovipositor," and, as in *brunneus* and *linearis*, it arises from the venter.

It might also be observed that in *Anobium punctatum* De Geer, Stein describes two accessory glands—in the female, of course. One is unpaired and the other paired, the former lying ventral to the "ovipositor" and the latter pair apparently arising from within the inner sheath of the "ovipositor." Pygidial glands, such as have been found in both sexes of *brunneus*, are not mentioned by Stein.

NOTE ON THE MORPHOLOGY OF THE APEX OF THE ABDOMEN IN
LYCTUS BRUNNEUS STEPH.

This note is based upon a close study of the sections previously referred to, and of a series of balsam mounts of pupæ in various stages of development, as well as various preparations made from the beetles.

TEXT-FIG. 4.



Apex of the abdomen of three pupæ of *L. brunneus* from specimens prepared and mounted in balsam. A, ventral aspect of a female, early stage of development; B, dorsal aspect of the same, seen through the back of the slide. C, ventral aspect of a female, later stage of development; D, dorsal aspect of the same, seen through the back of the slide. E, ventral aspect of a male, late stage of development; F, dorsal aspect of the same, seen through the back of the slide. *an*, anus; *gen*, genitalia; *go*, gonopore; *7p*, seventh pleurite; 7-10, tergites; VII-X, sternites. All figures *camera lucida* outlines, $\times 66$.

* The opportunity to examine specimens of *Cis boleti* Scop. has recently occurred, and the cloacal stalk was found to be ventral to the ovipositor, as in *brunneus*.

Text-fig. 4 depicts the ventral and dorsal aspects of the apex of the abdomen of three pupæ. From these it is apparent that the external appendages of the genitalia in both sexes arise from a similar position, *i. e.* on the ninth sternite (IX) and towards the tenth; the gonopore (*go*) lies medianly between these appendages, and is situated on the ninth sternite.

In the female *L. brunneus* the last visible sternite—the fifth of systematists—is the true seventh sternite (VII) and corresponds with the seventh tergite (7) directly above it (Pl. 33. figs. 1 & 3). The pygidium represents part of the eighth segment with the cloacal stalk (*lr*) an invagination of the eighth sternite (VIII), and the paired rods (*sr*) are lateral invaginations of the eighth tergite (8). This conclusion is supported by the presence of the m^1 and m^2 series of muscles (Pl. 32. fig. 1), which would seem to be modified intersegmental muscles. For the position of attachment of the m^1 set is from the apex of the cloacal stalk to lateral positions near the beginning of the ninth segment—the basal portion of the “ovipositor”; whilst the m^2 set, which envelop the cloacal stalk, arise from the point of its invagination. Moreover, a part of the muscles enveloping the paired rods (*sr*, Pl. 32. fig. 1) are attached laterally to the base of the ninth segment, whilst the remainder of these muscles are attached to the point of invagination of each rod.

The “ovipositor” is, therefore, a double tubular prolongation of the ninth segment, tergites and sternites being indistinguishable. Whether the transparent and setæ-less basal portion of the “ovipositor” represents a prolongation of the “soft membrane” between segments 8 and 9, is not manifest. Intersegmental membrane is not manifest anywhere else. And, conversely, with regard to the setæ-covered distal portion of the “ovipositor,” setæ are not manifest on any tergite but the seventh.

The apex of the ovipositor bears the anus dorsally between the fused and reduced tenth tergite and sternite, and it carries the genitalia on the ninth sternite beyond the anus.

In the male (Pl. 31. figs. 2 & 3) the last visible sternite is the seventh, as in the female; and likewise the pygidium represents the eighth segment. The ninth tergite and sternite are not solidly chitinized, and are invaginated and fused at their beginning to form the lumen enclosing the œdeagus and the anus, the latter being enveloped in a tube (*ev*, fig. 3) formed by the fused tenth tergite and sternite, as in the female. The invaginated ninth segment, the sternal portion of which is invaginated more than the tergal portion, shortly evaginates. Then the tergal portion joins the tergal portion of the tube [*ev* (10), fig. 3]; whilst the sternal portion, in which the gonopore is situated medianly, eventually joins the sternal portion of the tube (X, fig. 2). The ninth sternite is prolonged around the gonopore to form the extrusible membranous tube carrying the œdeagus, to which it is attached, as previously stated, around the basal piece. The paired rods (*vr*, figs. 1 & 3) that project into the abdomen from the tube (*ev*) are invaginations of the

tenth segment, and the three sets of muscles associated with these paired rods are also intersegmental muscles. The lateral sets following the course of the rods represent the muscles of the tenth sternite and tergite, whilst the median set represent those of the tenth and ninth sternite.

The homology between the genitalia of the sexes seems apparent (text-figs. 3 & 4 and Pl. 31, figs. 1 & 3). The sensory-pitted unjointed lateral lobes homologize with the sensory-pitted jointed vaginal palps; the basal pieces correspond; and the evaginated median lobe and extrusible internal sac homologize with the internal forked rods—"seitenstück"—and invaginated uterus. The analogy of their functions is obvious.

In the larva of *L. brunneus* there are nine pairs of spiracles: one prothoracic and eight abdominal pairs. In the adult there are nine pairs of spiracles: one prothoracic, one metathoracic—on the soft integument below the wing-bases—and seven abdominal pairs.

SUMMARY.

Both sexes in *L. brunneus* are sexually mature when they have emerged through the wood from their pupal chambers. An external sex-character is described.

In the male the reproductive organs consist of two testes of twelve pyriform testicular follicles of unequal size, six arising from each convoluted vas deferens, which terminate in a pair of jointed subcylindrical seminal vesicles. A short tube arises from each seminal vesicle, and forms the ejaculatory duct which empties into the œdeagus. Partly superimposed over the seminal vesicles and emptying into the short tubes are the paired accessory glands. They are subcylindrical, slightly tapering, and are curved around to underneath the ejaculatory duct. There is a pair of pygidial glands.

In the female the reproductive organs consist of two ovaries, each composed of fourteen ovarian tubes with the nutritive cells situated at their apices. The ripe eggs accumulate in a calyx which continues to form the oviduct. The oviducts terminate in a chitinized setæ-lined paired valve which forms the source of the common oviduct. At this point the voluminous spermatheca arises; it terminates in a tubular spermathecal or accessory gland. The common oviduct disappears into the invaginated double tubular "ovipositor" at a point in the metathorax, where the rectum also enters.

In the testicular follicles the spermatozoa are in bundles, in the spermatheca they are in packets or spermatophores.

The "ovipositor" has been found to consist of a double tubular prolongation of the ninth abdominal segment, with a reduced tenth segment towards the apex. When extruded the "ovipositor" is approximately the length of the beetle. Situated at the apex of the "ovipositor" are the genitalia with the anus a short distance behind.

Arising as an invagination of the eighth sternite and extending into the metathorax is the long, flexible, and strongly-chitinized cloacal stalk, from which arise systems of muscles for exerting and withdrawing the ovipositor. These muscles are found to be modified intersegmental muscles.

Morphologically the gonopore in both sexes was found to arise medianly on the ninth sternite, and the homology of the genitalia appears.

In the larva of *L. brunneus* there are nine pairs of spiracles, one thoracic and eight abdominal; in the adult there are also nine pairs, two thoracic and seven abdominal.

The movement which the rectum of the female is subjected to has been observed to be injurious to this organ, in that, lacking any muscular system for its withdrawal, other than its muscular structure, it was found convoluted inside the "ovipositor" of an egg-laying specimen. This defectiveness must accelerate death.

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EXPLANATION OF THE PLATES.

PLATE 31.

- Fig. 1. Male genitalia. Semi-diagrammatic. \times circa 51.
- Fig. 2. Transverse section (slightly oblique) through apex of abdomen of immature male. \times 100.
- Fig. 3. Right lateral aspect of apex of male abdomen. \times 114.
- Fig. 4. Diagrammatic ventral aspect of seminal vesicles, accessory glands and their junction with branched ejaculatory duct. \times circa 51.
- Fig. 5. Diagrammatic dorsal aspect of genitalia and alimentary tract *in situ*. Greatly magnified.

PLATE 32.

- Fig. 1. Female genitalia (*camera lucida*) and part of alimentary tract (partly diagrammatic). \times 51.
- Fig. 2. Longitudinal section through apex of female's abdomen. \times 384.
- Fig. 3. Transverse section through spermatheca. *C. l.* \times 384.
- Fig. 4. Longitudinal section through base of spermatheca and valves of oviduct. *C. l.* \times 384.

PLATE 33.

Arrangement *in situ* of genitalia and alimentary tract of female.

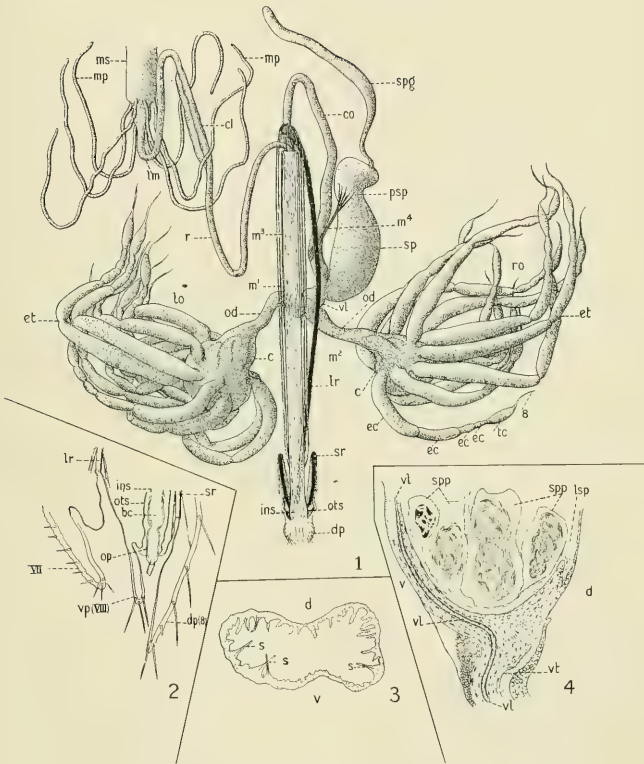
Partly reconstructed from sections and partly diagrammatic. Greatly magnified.

- Fig. 1. Left lateral view. Position of repose.
- Fig. 2. Dorsal view. Position of repose.
- Fig. 3. Right lateral view. Position when ovipositor extruded.

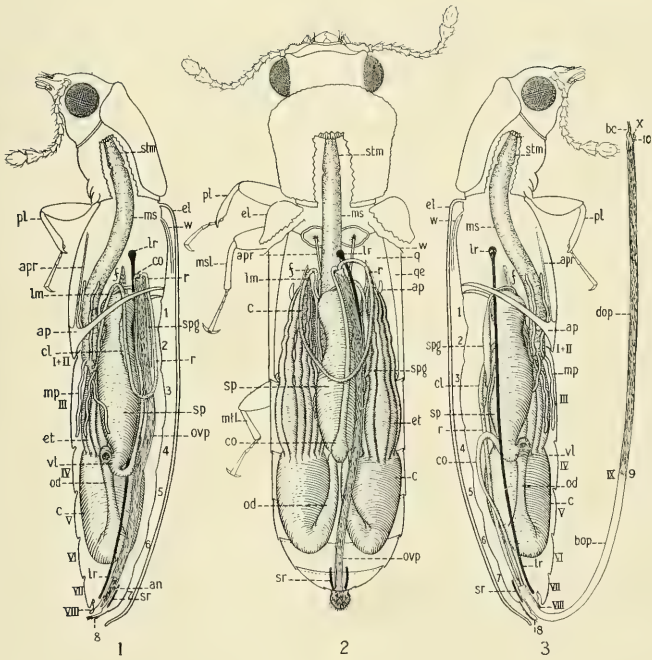
PLATE 34.

- Fig. 1. Longitudinal section through ovipositor at junction of inner and outer sheaths.
- Fig. 2. Longitudinal section through middle of ovipositor, showing rectum convoluted.
- Fig. 3. Longitudinal section through ovipositor, showing rectum and common oviduct separating.
- Fig. 4. Transverse section of ovipositor at junction of inner and outer sheaths.
- Fig. 5. Transverse section of middle of ovipositor.
- Fig. 6. Transverse section of ovipositor, showing rectum and common oviduct separating.
- Fig. 7. Transverse section of ovipositor showing anus free, and common oviduct completely enclosed by inner sheath.
- Fig. 8. Transverse section through bursa copulatrix.

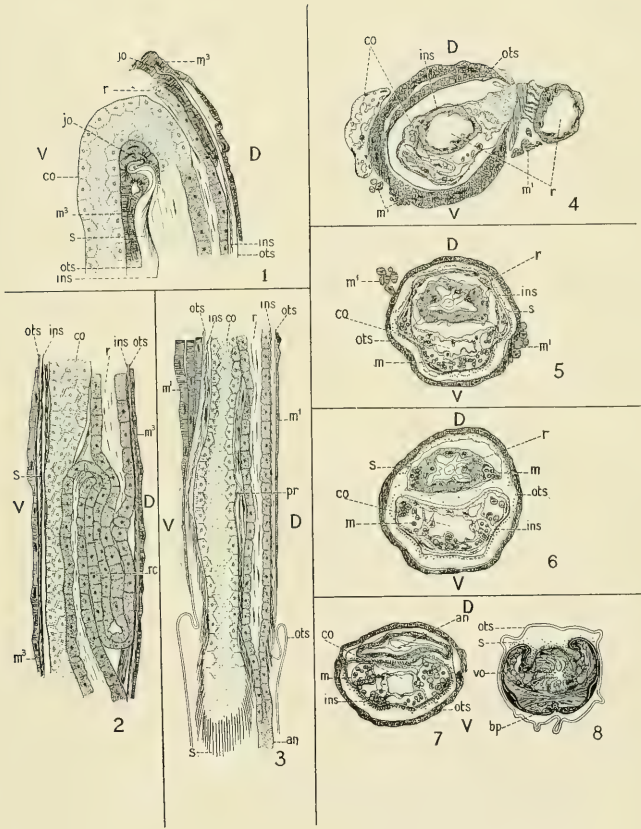
(Figs. 1, 2, and 3 are of a mature fertilized female. Part *C. l.* and partly reconstructed, Figs. 4, 5, 6, and 7 are of an immature female, *C. l.* Fig. 8 is of a fertilized female, *C. l.* All figures \times 840.)



GENITAL SYSTEM OF LYCTUS.



GENITAL SYSTEM OF LYCTUS.



GENITAL SYSTEM OF LYCTUS.

REFERENCE LETTERING.

ag, accessory gland; *age*, junction of accessory gland and ejaculatory duct; *an*, anus; *asg*, aperture of secreting glands; *ap*, apodeme; *apr*, rod of apodeme; *bc*, bursa copulatrix; *bop*, basal portion of ovipositor; *bp*, basal piece; *c*, calyx; *cl*, colon; *co*, common oviduct; *cm*, commissure; *d*, dorsal; *dop*, distal portion of ovipositor; *dp*, dorsal pygidial plates (8th tergite); *dr*, dorsal rod; *ec*, egg-chambers; *ej*, ejaculatory duct; *el*, elytron; *et*, ovarian tubes; *ev*, enveloping sheath; *f*, filament; *in*, integumental sheath; *ins*, inner sheath of ovipositor; *is*, internal sac; *jej*, junction of ejaculatory duct; *jo*, junction of outer and inner sheaths of ovipositor; *ll*, lateral lobes; *lm*, ileum; *lo*, left ovary; *lr*, cloacal stalk; *lsp*, loose spermatozoa; *m*, muscles; *m¹-m¹*, sets of muscles; *ma*, mesothoracic acetabula; *mc*, mesothoracic coxa; *mf*, median foramen; *ml*, median lobe; *mo*, median orifice; *mp*, malpighian tubes; *ms*, mesenteron; *msl*, mesothoracic leg; *mta*, metathoracic acetabula; *mtc*, metathoracic coxa; *mtl*, metathoracic leg; *mx*, suture between meso- and metasternum; *n*, abdominal nerve-ganglion; *od*, oviduct; *oe*, oedeagus; *op*, 2-jointed vaginal palp of ovipositor; *ots*, outer sheath of ovipositor; *ovp*, ovipositor; *p*, palp; *pa*, point of articulation; *pl*, prothoracic leg; *pr*, point of extrusion of anus; *psp*, setæ inside spermatheca; *q*, metasternum; *qe*, episternum of metasternum; *r*, rectum; *rc*, convoluted rectum; *ro*, right ovary; *s*, setæ; *sg*, secreting glands; *sp*, spermatheca; *spp*, packets of spermatozoa (spermatophores); *sr*, short rod; *st*, branch of ejaculatory duct; *stm*, stomodeum; *sv*, seminal vesicle; *tc*, terminal chamber; *ts*, testes; *v*, ventral; *vd*, vas deferens; *vo*, vaginal orifice; *vp*, ventral pygidial plate (VIII sternite); *vr*, ventral rods; *vt*, valvular duct; *w*, wing; 1-10 tergites, I-X sternites.